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A habitat suitability analysis at multi-spatial scale of two sympatric flying fox species reveals the urgent need for conservation action

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Abstract In this study we used a multi-spatial scale approach to investigate habitat suitability, roosting characteristics, and ecological niche in two flying fox species on the Comoros Islands—*Pteropus livingstonii* and *Pteropus seychellensis comorensis*. At a broad scale, we assessed the ecological niche and habitat suitability for both species using the Species Distribution Modeling method based on the recent ensembles of small models (ESM) approach. At a fine scale, Ecological Niche Factor Analysis (ENFA) was applied to assess habitat selection by each species. Direct observation was used at each roost to estimate the total number of individuals and to identify the roost characteristics. At both broad and fine scales, the analyses highlighted clear niche partitioning by the two species. We found that *P. livingstonii* has a very limited distribution, restricted to steep, high-elevation slopes of the islands' remaining natural forests, and the patterns were the same for roosting, foraging sites and the entire habitat. By contrast, *P. s. comorensis* has a relatively large geographic range that extends over low-elevation farmlands and villages and it was negatively correlated to natural forest across the entire area and all roosting sites, but its foraging areas were positively correlated to natural forest and high elevation areas. Both species selected large, tall trees for roosting. The total number of individuals in the studied area was estimated to be 1243 *P. livingstonii* and 11,898 *P. s. comorensis*. The results of our

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study demonstrated that these two species use different habitat types and ensure different ecosystem services in pollination and seed dispersion and thus are both critical for maintaining overall ecosystem dynamics. However, the currently high level of hunting pressure and roost disturbance makes them vulnerable to extinction. To ensure the viability of both species, conservation measures need to be taken by the Comoros government.

Introduction

Many ecosystem services provided by wild animals are fundamental to human societies due to their ecological and economic importance in the effective functioning of agriculture or natural forests (Giannini et al. 2012; Reid et al. 2013; Aziz et al. 2016).

It has been estimated that over 90% of the 2,50,000 flowering plant species depend on pollinators and that three-quarters of the 100 most cultivated plants and consumed by humans are pollinated by animals (Ingram et al. 1996). Natural forests also depend on animals, especially those that feed on fruit and pollen, such as birds and mammals which favor the dispersion of pollen and seeds, contributing to maintaining the structure of natural vegetation, genetic connectivity, and ecosystem regulation (McConkey et al. 2012). Today, ecosystems on a global scale are subject to human alteration caused by the conversion of natural ecosystems to agricultural land (Jantz et al. 2015). This change in land use combined with hunting and poaching have led to a dramatic decline of animals in the affected areas (Ripple et al. 2016). This species loss in turn has an impact on ecosystem functioning.

Fruit bats are among the most important ecosystem service providers in the animal kingdom (Abedi-lartey et al. 2016). As pollinators and seed dispersers, they contribute significantly to the regeneration, reproduction and dispersal of plant seeds, and thus have a major impact on ecosystem dynamics (Giannini et al. 2012; Aziz et al. 2017). Among the fruit bats, the genus *Pteropus*, also known as the flying fox, includes 62 species, which are considered keystone species for tropical forest functioning (Kunz et al. 2011). For example, Kunz et al. (2011) reported that at least 139 genera from 58 families of plants are dispersed by flying foxes which are fundamental for tropical forests maintaining. Due to their long-distance movements from roosting to feeding sites, their large bodies, and the fact that they live in large colonies, flying foxes can disperse a large number of seeds over large distances, thus ensuring connectivity between fragmented forest areas (Abedi-lartey et al. 2016; Aziz et al. 2016). Moreover, flying fox species pollinate and disperse seeds of several plant species that have high economic or medicinal value: for example, *Tamarindus indica* and *Adansonia* sp. (Friday et al. 2011; Kaboré et al. 2011). Aziz et al. (2016) report that flying fox species disperse at least 289 species of plants, of which 186 provide direct economic benefits to humans, see also McConkey and Drake (2006).

Flying foxes are relatively diverse in their ecology, distribution and feeding behavior. Some are well adapted to degraded landscapes, feeding on crops or plantations and roosting near villages. These species provide services to humans by their actions on cultivated plants (McConkey et al. 2012). Other species depend on natural forests and contribute to the maintenance of these (Majumdar et al. 2016; Roberts et al. 2016). The complementary actions of different flying fox species on ecosystem functioning (including degraded

ecosystems) is an argument in favor of conserving their diversity in order to promote global ecosystem regulation (McConkey and Drake 2006; Ancillotto et al. 2014). However, like several other tropical and sub-tropical animal species of relatively large size, they are highly threatened by habitat degradation especially deforestation and fragmentation as well as hunting (Ancillotto et al. 2014).

Pteropus livingstonii and *P. seychellensis comorensis* are two bat species endemic to the Comoros Islands (Goodman et al. 2010). These two species can coexist in some of their roosting and feeding sites, but seem to differ in their ecology, diet and reproductive behavior (Trewhella et al. 2001). *Pteropus livingstonii* is confined to the remaining mountain forests of the Anjouan and Mohéli Islands, while *P. s. comorensis* is widely distributed over all four islands of Comoros, as well as Mafia Island (Cheke 2011). Both species are threatened by habitat loss on these islands (Sewall et al. 2007). Their habitats face intense anthropogenic pressures and are subject to the highest deforestation rate in the world, with an estimated rate of forest loss of 8–9% per year (FAO 2010; Boussougou et al. 2015). *Pteropus livingstonii* is classified as critically endangered on the IUCN Red List (International Union for the Conservation of Nature, Sewall et al. 2016). This is due to its small population (estimated at 1200 individuals) and small range (estimated at 113.6 km^2) (Daniel et al. 2016). *Pteropus s. comorensis* is listed as a 'Least Concern' species due to its wide distribution (Mickleburgh et al. 2008). The large body size of both bat species and the fact they live in large colonies means they are able to disperse a large quantity of seeds over wide areas (Hernández-Montero et al. 2015; Razafindratsima 2014), thus having a potentially crucial impact both on forest regeneration and the cultivation of plants. Yet despite their importance in ecosystem functioning in the Comoros, their ecology and, especially, their habitat requirements at different spatial scales are poorly known. Such knowledge is essential in order to establish relevant conservation plans.

The aim of this study was to identify the habitat requirements of these two flying fox species at two spatial scales. At a broad scale, we assessed the ecological niche and habitat suitability of both species using species distribution modeling (SDM) based on the recent Ensembles of Small Models (ESM) approach, which is particularly adapted to rare and localized species (Breiner et al. 2015). At a local scale, we investigated each species' habitat selection in terms of roosting characteristics. Finally, we used this information to identify the pressures on these two species and to propose actions crucially needed for their conservation.

Materials and methods

Study area

The Comoros archipelago is located in the Indian Ocean, midway between Madagascar and the eastern coast of Africa. This archipelago comprises four islands: Grande Comore, Mohéli, Anjouan (these three islands make up the Union of the Comoros), and Mayotte (an overseas department of France). Each of the islands is separated by a mean distance of about 60 km. Since their emergence some 8 million years ago, the islands have never been connected to a continental mainland nor to each other (Goodman et al. 2010). Due to their volcanic origin, these islands have considerable topographic variation (Michon 2016). Our study focused only on the three islands of the Union of the Comoros.

Data collection

Site selection

Fieldwork took place from November 2014 to April 2015 and from January to April 2016. The sampling locations for the collection of presence and absence data were selected according to different survey designs for the two species. For *P. livingstonii*, we gathered information regarding this species' roosting sites from available studies (Trewhella et al. 2001; Granek 2002; Louette et al. 2004; Sewall et al. 2007, 2011a, b; Goodman et al. 2010); local NGOs also provided precise information on *P. livingstonii* roosting locations. For this species, all forests where roosting sites had been previously observed were selected as study locations, resulting in 19 sampling sites (3 in Mohéli and 16 in Anjouan) (Table 1).

For *P. s. comorensis*, as no precise data regarding the habitat used by the species was available in the literature, we used maps (Google Earth and ArcGIS) as well as information obtained during interviews with the local population to select the different sampling locations. The selection of the sampling sites was also informed by our wish to sample areas in which a wide variety of habitats were available. This range of habitats is necessary when sampling occurrence data in order to compare sites in which a species is present with sites in which it is absent. The island of Grande Comore has two forests (Karthala forest in the center of the island, and La Grille forest in the north). These two forests were selected for the study as they include a spectrum of habitats, from preserved to degraded forests as well as agricultural lands. On the island of Mohéli, there is only one large forest in the center of the island—this, and the surrounding vicinity, was selected to sample occurrence data for this species. On both Anjouan and Mohéli, as *P. s. comorensis* is known to occur in sympatry with *P. livingstonii* in some locations, the forests where *P. livingstonii* is known to be present were selected. In addition, we selected the regions of Hajoho-Ngntranga and Bimbini (Anjouan) as these regions also include a range of habitats, such as forests, mangrove swamps and agricultural lands. For each forest selected as a sampling site, we then carried out interviews in all the villages located at a distance of 1–5 km from the forest to identify the precise locations of fruit bats. From our initial field observations and from reports in the literature (Trewhella et al. 2001), *P. s. comorensis* can be found in both villages and agricultural lands. Thus, for this species we sampled locations in the village, in agricultural lands, in degraded vegetation, and in the adjacent preserved forest. This resulted in 59 sampling sites (30 on Grande Comore, 15 on Mohéli, and 14 on Anjouan) for the presence–absence data collection for *P. s. comorensis*.

Presence of bats at the roosting sites

To collect occurrence data, all known *P.livingstonii* roosts and the *P. s. comorensis* roosts identified by local people during interviews were visited to check for the presence of bats. For both species, the prospection for potential roosts and counts were carried out during the day from 9:00 am to 12:30 pm by three or four observers. If a roosting site hosted fruit bats, a plot with a 25-m radius (see below) was delineated around the tree with the highest number of bats (when several trees were occupied), and the geographic location was recorded using a Global Positioning System (GPS).

Table 1 Number of *P. livingstonii* and *P. s. comorensis* individuals per site and per island; the first column represents the nearest town name; the co-occurrence (column Co-occur) of the two studied species (yes) is shown in bold; the heads of columns are also shown in bold; Nam.For: Name of the forests or exact sites where the data were collected

Nearest town name	Nam.For	Islands	P. liv-counts	S Period (dd. mm.year)	P. s. c-counts	S Period (dd. mm.year)	Co-occur
Ada		Anjouan	23	02.03.15	–		No
Bazimini		Anjouan	64	26.02.15	–		No
Dindri		Anjouan	4	24.02.15	33	24.02.15	**Yes**
Hombo		Anjouan	105	02.02.15	–		No
Kanagani	Kang 1	Anjouan	15	10.03.15	366	10.03.15	**Yes**
Kanagani	Kang 2	Anjouan	6	23.02.16	–		No
Kowé		Anjouan	63	11.03.15			No
Limbi		Anjouan	27	01.03.15	17	01.03.15	**Yes**
Lingoni		Anjouan	104	05.03.15			No
Mpagé		Anjouan	108	13.03.16			No
Mromaji		Anjouan	44	25.01.16	231	25.01.16	**Yes**
Moya		Anjouan	82	11.02.16	–		No
Outsa		Anjouan	8	03.03.15	69	03.03.15	**Yes**
Ouzini		Anjouan	81	09.02.16	128	09.02.16	**Yes**
Salamani		Anjouan	29	03.03.15	52	03.03.15	**Yes**
Salamani	Dziajou	Anjouan	3	09.03.15	–		No
Ouallah-Mirereni	Hakidogo	Mohéli	103	18.02.15	20	15.02.15	**Yes**
Ouallah-Mirereni	Hassera-Ndrengé	Mohéli	349	17.02.15	–		No
Nioumachouwa		Mohéli	25	04.03.16			No
Ajoho		Anjouan	–		11	09.02.16	No
Bambao mtsanga		Anjouan	–		40	03.02.16	No
Bimbini		Anjouan	–		126	05.02.15	No
Chaweni		Anjouan	–		2	07.02.16	No

Table 1 (continued)

Nearest town name	Nam.For	Islands	P. liv-counts	S Period (dd. mm.year)	P. s. c-counts	S Period (dd. mm.year)	Co-occur
Djimlime		Anjouan	–		71	06.02.16	No
Domoni		Anjouan	–		159	10.02.16	No
GG		Anjouan	–		37	03.02.16	No
Mahale		Anjouan	–		69	08.02.16	No
Mremani		Anjouan	–		39	07.02.16	No
Mutsamudu		Anjouan	–		249	25.02.15	No
Nyatranga		Anjouan	–		202	04.02.16	No
Ongojou		Anjouan	–		48	07.02.16	No
Ongoni		Anjouan	–		239	07.02.16	No
Sima		Anjouan	–		157	05.02.16	No
Bandamadji		G.Comore	–		110	17.01.15	No
Bangwa		G.Comore	–		88	21.08.16	No
Chezani		G.Comore	–		78	19.08.15	No
Djomani_Chamlé		G.Comore	–		731	02.03.15	No
Fassi		G.Comore	–		52	03.03.15	No
Foumboudzivouni		G.Comore	–		162	18.01.15	No
Itsandra		G.Comore	–		124	04.02.15	No
Itsandzeni		G.Comore	–		40	06.02.15	No
Itsinkoudi		G.Comore	–		98	10.08.16	No
Itsoundzou		G.Comore	–		134	28.12.14	No
Maweni-Ivembeni	LaGrille	G.Comore	–		70	31.03.16	No
Madjoma		G.Comore	–		98	17.01.15	No
Mbeni		G.Comore	–		270	15.08.16	No
Mboude-Dimani		G.Comore	–		185	17.01.15	No
Mde		G.Comore	–		156	13.01.15	No

Table 1 (continued)

Nearest town name	Nam.For	Islands	P. liv-counts	S Period (dd. mm.year)	P. s. c-counts	S Period (dd. mm.year)	Co-occur
Mdjoiyezi		G.Comore	–		437	11.01.15	No
Midjendjeni		G.Comore	–		742	18.01.15	No
Mitsamihouli		G.Comore	–		80	24.08.16	No
Mohoro		G.Comore	–		162	15.01.15	No
Moindzaza		G.Comore	–		355	27.12.14	No
Moroni		G.Comore	–		364	13.01.15	No
Mtsangadjou		G.Comore	–		48	12.12.14	No
Nioumadzaha	Nioum 1	G.Comore	–		503	03.12.14	No
Nioumadzaha	Nioum 2	G.Comore	–		670	06.12.14	No
Ntsaoueni		G.Comore	–		629	03.01.15	No
Pidjani		G.Comore	–		72	17.01.15	No
Sada		G.Comore	–		249	23.08.16	No
Sadani-Oichili		G.Comore	–		103	10.08.16	No
Salimani-Hama		G.Comore	–		109	13.08.16	No
Sidjouwou		G.Comore	–		121	17.01.15	No
Barakani		Mohéli	–		162	04.03.16	No
Boingoma		Mohéli	–		79	07.03.16	No
Damou		Mohéli	–		690	09.03.15	No
Djando		Mohéli	–		185	19.03.16	No
Djoyezi		Mohéli	–		79	14.03.16	No
Fomboni		Mohéli	–		108	05.03.16	No
Hamba		Mohéli	–		148	12.03.16	No
Howani		Mohéli	–		199	21.03.16	No
Miringoni		Mohéli	–		81	24.03.16	No
Moihani		Mohéli	–		37	20.03.16	No

Table 1 (continued)

Nearest town name	Nam.For	Islands	P. liv-counts	S Period (dd. mm.year)	P. s. c-counts	S Period (dd. mm.year)	Co-occur
Ndremeani		Mohéli	–		115	23.03.16	No
Ndrondroni		Mohéli	–		232	06.03.16	No
Nioumachouwa		Mohéli	–		152	03.03.16	No
Ouallah 2		Mohéli	–		375	17.02.15	No
Wanani		Mohéli	–		82	17.03.16	No
Total count on Anjouan			766		2114		
Total count on Grande Comore			–		7040		
Total count on Mohéli			477		2744		
Overall total			1243		11,898		

S Period sampling period, *P.s.c Pteropus seychellensis comorensis*, *Co-occur* co-occurrence, *P.liv Pteropus livingstonii*

Presence of bats at the foraging sites

To locate fruit bats at foraging sites, the prospection was carried out at dusk and after nightfall from 16:30 to 19:30 pm. In each location, data was collected (when available) along trails and roads in open areas suggested by our local guides. Whenever possible, we selected routes that crossed different types of habitat (preserved forest, degraded forest or agricultural land) to allow the detection of fruit bats in different habitats within a geographical area. The aim was to facilitate the identification of the habitat preferences of the studied species. In dense vegetation, transects from 1 to 2 km in length were cleared by our team. The starting point of a transect was randomly selected and the trail followed the altitudinal gradient. Transects were generally not linear as we were often forced to bypass valleys and mountains. During each prospection, when a flying fox was observed at a distance of between 0 and 50 m from the center of a transect (the distance varied depending on visibility), a plot with a 25-m radius was delineated around the tree hosting the bats and the geographic location was recorded. During the dusk/nightfall surveys, a site was considered to be absent of bats if no individuals were observed during 30 min of prospection. After this duration, a 25-m radius plot was delineated to define the location.

Habitat characteristics

Habitat characteristics such as forest type (natural or degraded), density of trees, canopy height, canopy openness, and intensity of tree cutting were recorded for each of the 25 m radius plot. Tree density was considered as the number of trees with a diameter at breast height (dbh) of more than 15 cm. Intensity of tree cutting was estimated by counting the number of trees felled down in each plot. Tree height and dbh were recorded for each tree that hosted bats. Tree height and the percentage of canopy openness were visually estimated by 3–4 people (two experienced researchers from our team and one or two local guides) and the mean value was recorded. These estimations are prone to errors, yet we were expecting differences between occupied and unoccupied sites far larger than the imprecision of the measure. The dbh of each tree was measured using a tape measure. The vernacular name of the roosting tree species was provided by the local guides and confirmed by our local assistants. The scientific names of the plants were later identified from their vernacular names in the University of Comoros herbarium laboratory.

Our sampling sessions were carried out during 169 days in the three islands of Comoros: 75 days in the Grande Comore (44 sampling days in agricultural lands, degraded vegetation at low elevation and 31 days in forests at high elevation), 53 days in Ajouan (24 sampling days in agricultural lands, degraded vegetation at low elevation and 29 days in forests at high elevation) and 41 days in Mohéli (18 sampling days in plantation fields, degraded vegetation and 23 days in forests at high elevation). In the Grande Comore Island, sampling was mostly conducted in agricultural lands and degraded vegetation at low elevation because roosts of *P. s. comorensis* are usually found in these areas. In Anjouan and Mohéli islands, the sampling was spread equally in the different type of habitats, since the two species we studied here were located in different types of habitats (*P. livingstonii* at high elevation and *P. s. comorensis* at low elevation).

Roosting counts

We counted individuals using binoculars at a distance of 20–100 m from each roosting tree. These counts were carried out from 9:00 to 12:30 p.m., a period during which flying foxes are inactive (Trewhella et al. 2001). Each member of the team performed multiple counts, and the final population estimate was the average number of individuals given by the four observers.

Ecological niche modeling at a broad scale

We used ecological and topographic predictors with presence-only data to perform SDM at a broad scale. Predictors were selected based on our own knowledge of the ecology of these species, on the literature (Trewhella et al. 2001; Sewall et al. 2011b), and on interviews conducted with the local population. We considered nine variables (seven ecological and two topographic variables). As Grande Comore and the other two studied islands are very different in terms of ecological and topographic contexts, we built separate models for Grande Comore and for the Anjouan–Mohéli group of islands. The selected variables were elevation and slope, and distance from intact natural forest, degraded vegetation, a cultivated area, the nearest village, the nearest roads, basaltic rock (Grande Comore only) and permanent or temporary rivers (Anjouan and Mohéli only). Ecological and anthropogenic variables were extracted from a georeferenced general layer map developed by Hawlitschek et al. (2011) resampled to a 25 m pixel resolution using ArcGIS software. The elevation and slope were extracted from 90 m digital elevation model data from the NASA Shuttle Topographic Mission (US Geological Survey 2004) also resampled to a 25 m pixel resolution.

Three different analyses are carried out during this study for both flying fox species. First, we performed an analysis using all the records in order to have the global distribution for each species. Second, we performed analyses using records of (1) roosting and (2) foraging sites which allow us to evaluate the habitat requirements of the two flying fox species in terms of roosts and forage at a broad scale.

Statistical analysis

Species distribution modeling using ensemble of small models

As *P. livingstonii* is a rare and elusive species and its number of known roosting sites is low (21 roosting sites according to Sewall et al. 2007; Daniel et al. 2016), the occurrence data for this species was very low. The combination of limited occurrence data and a large number of predictors (here, 9) in SDM can lead to model overfitting (Breiner et al. 2015). To work around these limitations, some researchers reduce the number of predictors by removing certain variables from the analysis (usually those most correlated), but this can lead to loss of information. To overcome this difficulty, we used the recent method of ensembles of small models (ESMs) (Breiner et al. 2015). This approach consists of fitting all potential bivariate models (28 in our case) and then averaging them using weights based on model performance (Breiner et al. 2015). We used Generalized Linear Models (GLMs) with binomial distribution and a logit link to build our SDMs (Guisan et al. 2002). GLM is well established for modeling species distribution and evaluating ecological niche and has

been widely implemented with presence and absence data as well as with presence-only data in the context of SDM (Crawford and Hoagland 2010; Guisan et al. 2002). As accurate absence data was not available to build such a model in our case, a collection of pseudo-absences was sampled in the entire areas at island scale to fit the model (Barbet-Massin et al. 2012). According to Barbet-Massin et al. (2012), models fitted with a large number of randomly sampled pseudo-absences produced the most accurately predicted distribution. In our study, we randomly sampled 2000 pseudo-absences from the entire study area to fit our model (entire data set). For the SDM on the roosting and foraging analyses, 1000 pseudo-absence points were randomly sampled in the entire areas of the different islands or group of islands of Comoros (see above) to fit the ESMs due to the small amount of occurrence data. We then considered 80% of the data to run the model and 20% for the model evaluation. We ran the model using 100 repetitions of random pseudo-absence selection (Guisan and Thuiller 2005). The model's predictive performance was assessed using the area under the curve (AUC) of the receiver operating characteristic (ROC) (Phillips et al. 2006). These indices evaluate the ability of the model to differentiate between sites where a species is present and those where it is absent. Models with an AUC value close to 1 are considered perfect predictors of the observed data, while models with a value around 0.8 are considered good predictors (Elith et al. 2006). We also examined sensitivity (true positives) and specificity (false negatives) to evaluate model performance and accuracy. To estimate the surface area of suitable habitats for the two species and their niche overlap, the continuous maps of species distribution generated by our ESMs were converted into binary maps (suitable/unsuitable) using threshold values obtained using the higher true skill statistic approach (HTSS) as recommended by Liu (Liu et al. 2013).

Habitat selection at small scale

To model habitat selection at plot scale, we performed an Ecological Niche Factor Analysis (ENFA), a method based on the Hutchinson niche theory (1957) and defining the ecological niche of a species as a hypervolume in the multidimensional space of environmental variables in which the species is able to maintain a viable population (Basile et al. 2008). These analyses quantify marginality and specialization, allowing the comparison of realized niches within the available environmental conditions (Hirzel et al. 2002). More specifically, marginality describes the difference between a species' habitat use and the average environmental conditions in the study area, while specialization measures the narrowness of the niche (Basile et al. 2008). The ENFA were performed using a combination of presence and absence data collected in the foraging sites and a set of four landscape metrics: canopy height, canopy openness, tree density and tree cutting collected also in the level of each plot of foraging site. A permutation test (with 1000 permutations) was performed for marginality to test for its significance. In addition to ENFA, we performed a Spearman's rank test to test the correlation between the number of fruit bats and both dbh and tree height at the scale of a dormitory. Statistical tests were considered significant when the p value was < 0.05. All analyses were conducted using Environmental R 3.3.2 (R Development Core Team 2016) with the Ecospat package (Broennimann et al. 2015) and Biomod2 package (Thuiller et al. 2016) for SDM at the broad scale, and the ade4 and adehabitat packages (Calenge 2006; Dray and Dufour 2007) at the plot scale.

Results

Pteropus s. comorensis

The number of individuals ranged between 11 and 742 per colony, with an average of 184 individuals per colony. In total, we observed 11,898 individuals at 59 different sites on the three islands (Grande Comore, Anjouan and Mohéli, Table 1).

A total of 76 occurrences were recorded on Grande Comore, 43 and 33 occurrences data correspond to the roosting and foraging sites respectively. On this island, the model's AUC averaged to 0.87 ± 0.03 for the entire dataset, 0.90 ± 0.07 and 0.88 ± 0.06 for roosting and foraging site respectively, suggesting a good ability of the model to differentiate between species presence and absence. On the Anjouan–Mohéli group, 93 occurrences were recorded, 53 and 40 occurrences data correspond to the roosting and foraging sites respectively. On these islands, moderate AUC values averaged to 0.64 ± 0.05 for the entire dataset, 0.68 ± 0.07 and 0.68 ± 0.08 for roosting and foraging sites respectively were obtained for this species. Mean sensitivities were high for the three models (sensitivity $= 0.88 \pm 0.07$, 0.96 ± 0.03, 0.86 ± 0.02 for the entire dataset, roosting and foraging site respectively in Grande Comore and 0.84 ± 0.07, 0.81 ± 0.08 and 0.81 ± 0.03 02 for the entire dataset, roosting and foraging sites respectively in Anjouan–Mohéli group), whereas mean specificities were high on Grande Comore (0.79 ± 0.01, 0.78 ± 0.02 and 0.88 ± 0.01 for the entire dataset, roosting and foraging sites respectively), but low for Anjouan–Mohéli (0.45 ± 0.02, 0.54 ± 0.03 and 0.59 ± 0.03 for the entire dataset, roosting and foraging sites respectively).

Based on the SDMs and response curves of the entire data set, the results indicated that optimal habitats for this species are areas close to villages and roads, near degraded forests and plantations. This pattern was the same for Grande Comore and Anjouan–Mohéli islands (Figs. 1, S1). The results of the SDMs based on datasets splitted in foraging and roosting sites are quite different (Figs. 2, S2). According to response curves, *P. s. comorensis* avoids primary and mountain forests for roosting sites of the three islands (Grande Comore, Anjouan and Mohéli, Figs. 3, 4). In contrast, the species uses natural forest and high elevation for foraging in Anjouan and Mohéli (but not in the Grande Comore where the species still avoids primary and mountain forests for both roosting and foraging sites, Figs. 2, 4). On Grande Comore, the predicted suitable area (with the entire data set) for *P. s. comorensis* is a narrow continuous band close to the coast, extending from southern to northern regions (Figs. 5, S2). This suitable area estimated with the entire dataset is estimated to cover 206 km^2; encompassing different types of habitats that include degraded land, cultivated areas, and villages. We estimated a suitable habitat of 233 and 182 km^2 for the roosting and foraging sites respectively. For the Anjouan–Mohéli group, the suitable area with all the dataset but also with the roosting site data for this species covers the entire lowlands, including all villages, agricultural areas, and degraded vegetation (Fig. 6). In the contrast, the suitable area with the occurrence data collected in foraging sites covers the entire lowlands, some elevation areas, some natural forests, all villages, agricultural areas and degraded forests. The area is estimated to cover 420 km^2 for the entire dataset, 233 and 506 km^2 for the roosting and foraging site respectively.

The permutation test for marginality in the ENFA model was significant ($p < 0.05$).

However, both marginality and specialization were relatively low (0.50 and 1.85 respectively). Tree cutting and canopy height represented the most explanatory predictors for the two axes of the ENFA (Fig. 7b). Tree cutting was positively correlated to the marginality axis (correlation coefficient of marginality: $r = 0.67$). Canopy height was
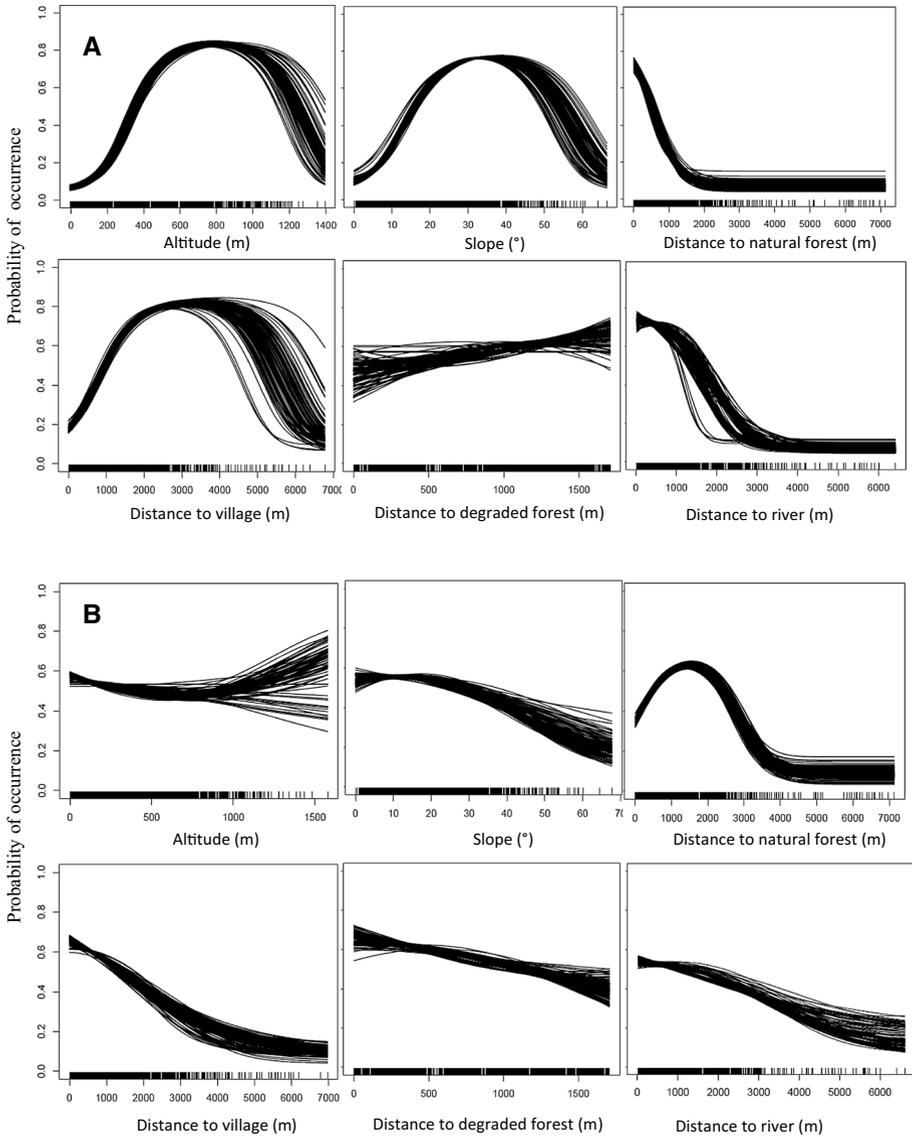
Fig. 1 Relationships between Comorian flying fox occurrence probability (based on the entire data set) and ecological/topographic predictors according to the ensembles of small models (ESM) approach; **a** *P. living-stonii*, **b** *P. s. comorensis*

positively correlated to the specialization axis (correlation coefficient of specialization: r = 0.84), indicating that this species preferentially selects habitat with a high canopy.

We recorded 22 different plant species used as roosts by *P. s. comorensis* (Table S1). The number of individuals at a roosting site was correlated to both plant height and dbh (Spearman correlation test: S = 19,948, p < 0.01 for plant height and S = 1,628,000,
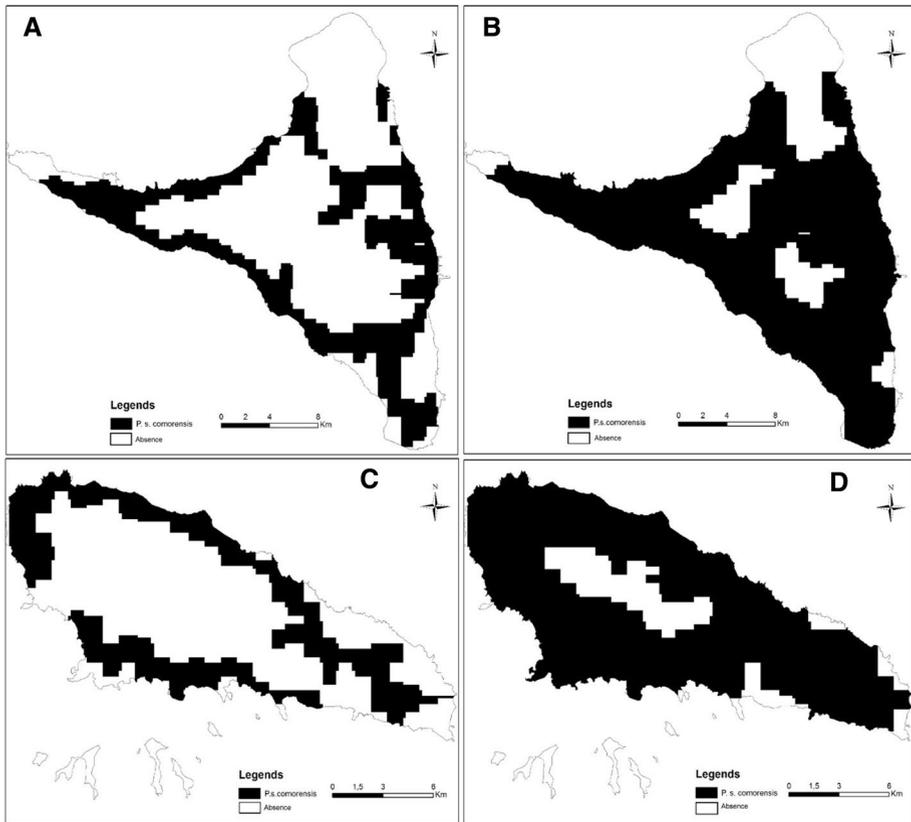
Fig. 2 Predicted suitable habitat for *P. s. comorensis* on Anjouan and Mohéli Islands; **a** roosting habitats in Anjouan, **b** foraging habitats in Anjouan; **c** roosting habitats in Mohéli; **d** foraging habitats in Mohéli

p < 0.001 for dbh), indicating that *P. s. comorensis* preferentially roosts on large, tall trees (mean occupied tree height = 23.98 ± 6.4 m and mean dbh = 86.46 ± 49.48 cm).

Pteropus livingstonii

The colonies of *P. livingstonii* ranged between 3 and 349 individuals, with an average of 65 individuals per colony. We observed a total of 1243 individuals during our field surveys of 19 locations (Table 1). For this species, we recorded a total of 51 occurrences on the Anjouan–Mohéli islands (the full dataset) and 19 occurrences of roosting sites and 32 occurrence data in the foraging sites. For this species, SDM performance had an average AUC value of 0.85 ± 0.03, indicating good model performance when the entire data was modeled. Regarding the roosting and foraging sites, the model had average AUC values of 0.84 ± 0.05 and 0.85 ± 0.05 respectively.

Mean sensitivity and specificity showed high values both for the entire data set (mean sensitivity = 0.94 ± 0.05; mean specificity = 0.74 ± 0.02), for roosting sites data (mean sensitivity = 0.98 ± 0.01; mean specificity = 0.70 ± 0.03) and foraging sites (mean sensitivity = 0.93 ± 0.05; mean specificity = 0.76 ± 0.02). Response curves for the roosting
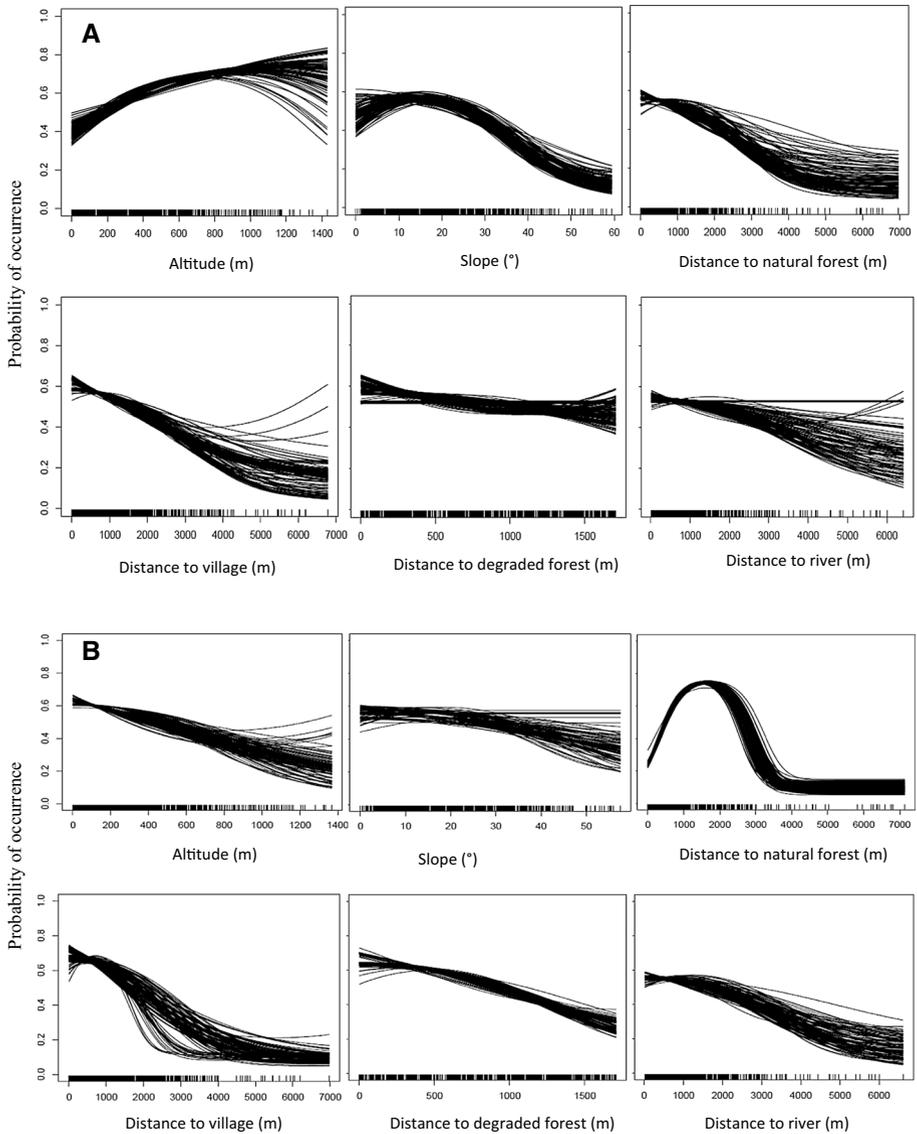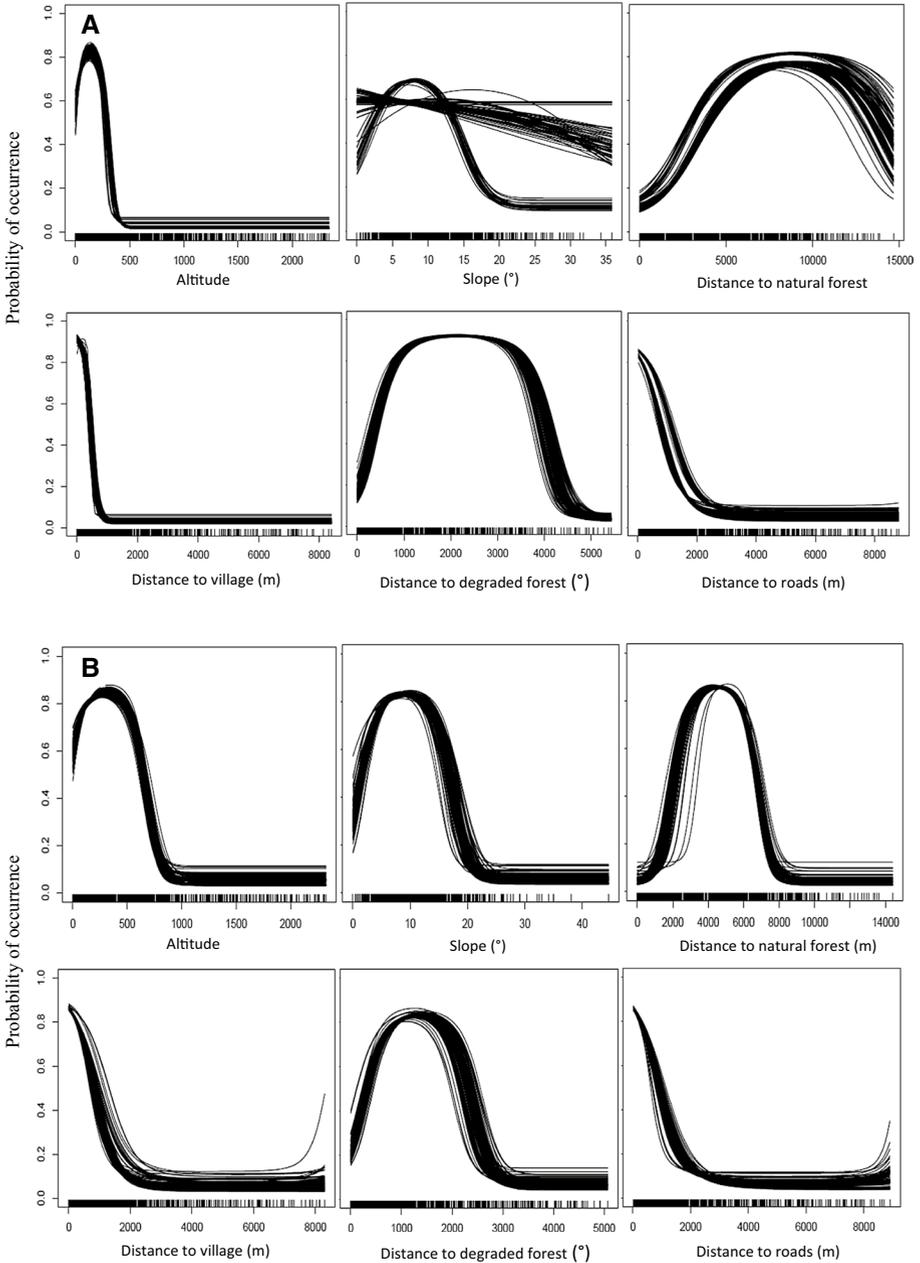
Fig. 3 Relationship between *P. s. comorensis* occurrence probability (Anjouan and Mohéli Islands) and ecological/topographic predictors according to the ESMs approach; **a** roosting habitat, **b** foraging habitat

and foraging sites and the entire occurrence dataset showed similar patterns (Figs. 1a, 8). Detailed examination of the response curves revealed that the most suitable habitats for *P. livingstonii* are found in natural forests, on steep slopes ranging from 30 to 50°, at altitudes ranging from 500 to 1100 m above sea level, and in proximity to a river and the patterns were the same for the entire dataset, roosting and foraging sites (Figs. 1a, 8, 9).

The predicted suitable habitat area for Livingstone's fruit bats was restricted to the central regions of Anjouan and Mohéli Islands, i.e. primary, mountainous forests, with a total

Fig. 4 Relationship between *P. s. comorensis* occurrence probability (Grande Comore Island) and ecological/topographic predictors according to the ESMs approach; **a** roosting habitat, **b** foraging habitat

surface area estimated at 160 km² for the entire dataset, 189 and 160 km² for roosting and foraging site respectively. On Anjouan Island, this area included all remaining primary forests, some degraded forests in the northern region of Nioumakelé (including Adda and
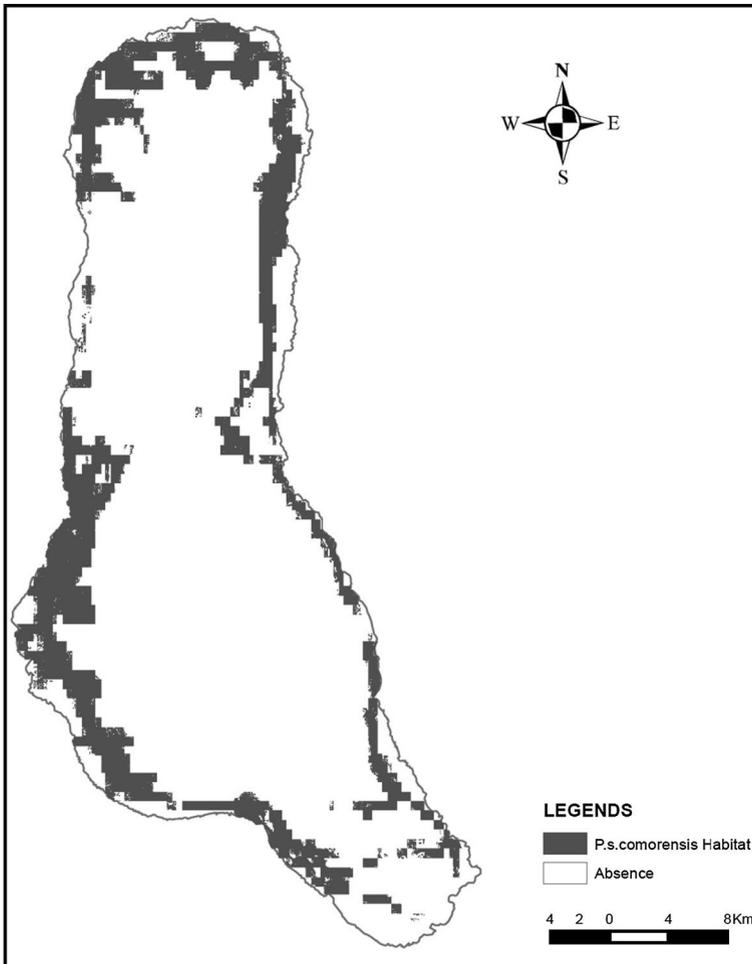
Fig. 5 Predicted suitable habitat for *P. s. comorensis* on Grande Comore Island (based on the entire data set)

Ouzini forests, and the forest of the eastern part of Limbi), the forest located in the northern region of Moya (Moya, Nindri-Kowe and Lingoni forests) as well as the forest of Mpage and Mdjimandra. A few small areas of high suitability were predicted in the northern part of the island, including the forest located near Gnantranga village, although *P. livingstonii* has never been reported in this area. On Mohéli Island, the predicted suitable area for this species was restricted to the primary forest and some degraded forests of Mledjele in the central part of the island. This area includes the forest located north of Miringoni village in the west of the island, and the forest located west of Siri-Ziroudani village in the east of the island (Fig. 6). Due to the large difference in ecological niche and habitat requirements of the two bat species, their suitable area overlaps by only 7.40 km² (the entire data set).

The permutation test for marginality in the ENFA was significant ($p < 0.05$). Overall, marginality and specialization were low (0.20 and 1.85 respectively). Of the four landscape metrics used to evaluate potential distribution, two variables contributed most to
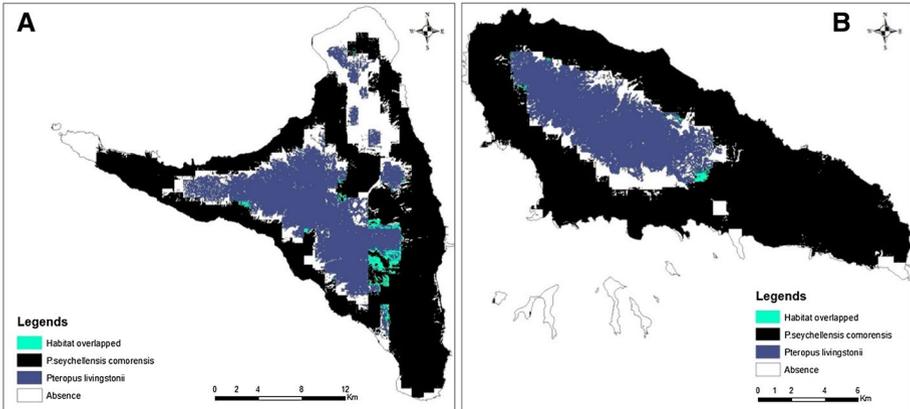
Fig. 6 Predicted suitable habitat for *P. livingstonii* and *P. s. comorensis* (all the data set) *on* Anjouan (**a**) and Mohéli (**b**) Islands; Purple: *P. livingstonii* habitat; Black: *P. s. comorensis* habitat; Green: overlapped habitat by the two species; white: Absence of the two species
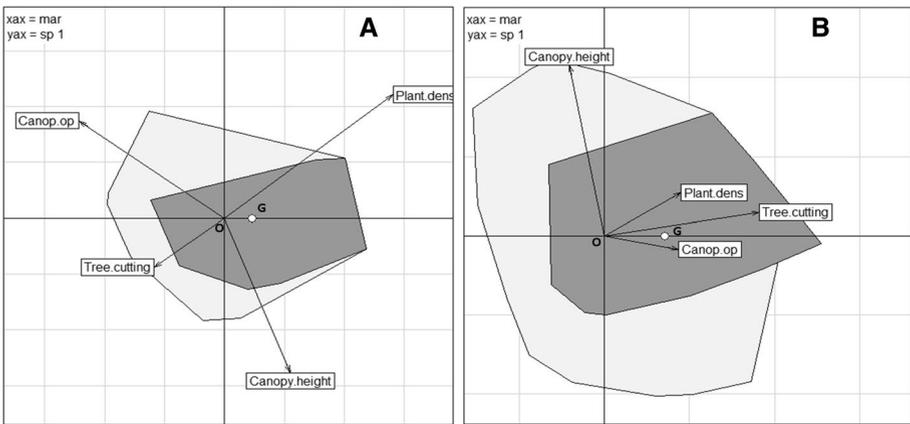

Fig. 7 Biplots of the Ecological Niche Factor Analyses (ENFA) showing potential distributions and the areas available for *P.livingstonii* (**a**) and *P. s. comorensis* (**b**); Light gray and dark gray regions represent, respectively, the minimum convex polygons of the available and used habitats; the x-axis (xax) represents the marginality axis (mar), and the y-axis (yax) corresponds to the first specialization axis (sp 1); the point (O) represents the centroid of the available habitat; the white dot (G) corresponds to the centroid of the used habitat; *Canopy.Op* canopy openness, *Plant dens* plant density)

marginality and specialization: canopy openness and tree density (Fig. 7a). Canopy openness was negatively correlated to the marginality axis (r = −0.60), while tree density was positively correlated to the first eigenvalue of specialization (r = 0.55) and to the marginality (r = 0.69). The distribution of *P. livingstonii* was thus found to be relatively limited to areas with high tree density and closed forest cover.

We recorded 16 different tree species used by *P. livingstonii* for roosting (Table S2). The number of individuals per roosting site was highly correlated to tree height (Spearman correlation test, S = 19,948, p < 0.01 and S = 1,765,800, p < 0.001), indicating that this species
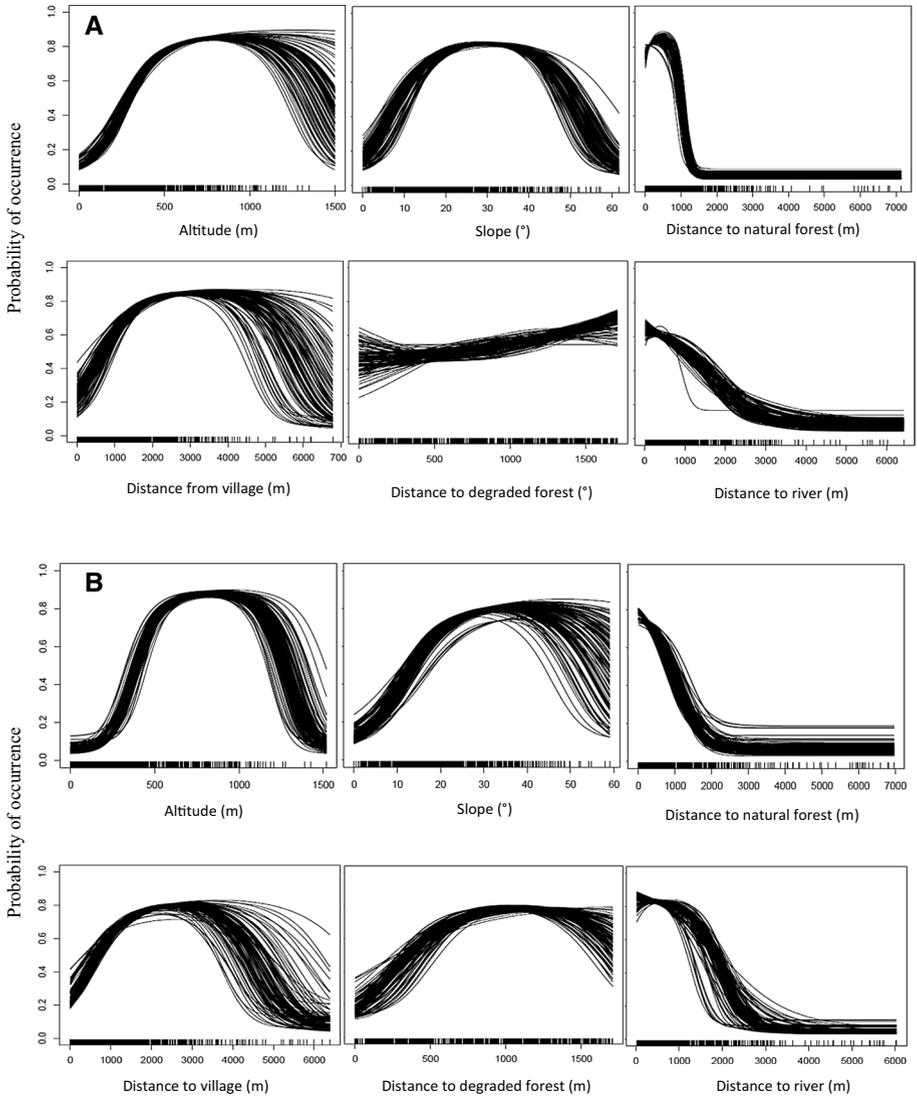
Fig. 8 Relationship between *P. livingstonii* occurrence probability and ecological/topographic predictors according to the ESMs approach; **a** roosting habitat, **b** foraging habitat
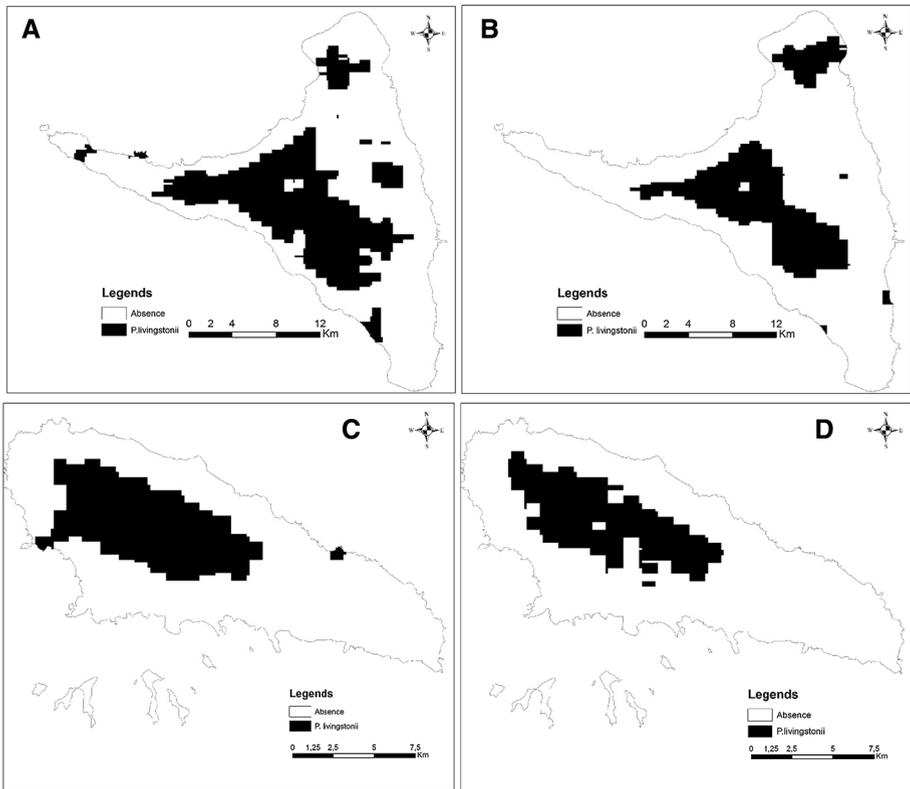
Fig. 9 Predicted suitable habitat for *P. livingstonii* on Anjouan and Mohéli Islands; **a** roosting habitats in Anjouan, **b** foraging habitats in Anjouan; **c**: roosting habitats in Mohéli; **d** foraging habitats in Mohéli

roosts preferentially on tall trees. No evidence of correlation between number of bats and tree dbh was observed (Spearman correlation test, S = 25,640, p = 0.21).

Discussion

Pteropus s. comorensis

A number of studies have suggested that habitats dominated by intensive agriculture within urban areas are used by many fruit bat species. For instance, *P. rufus* in Madagascar and *P. giganteus* and *Cynopterus sphinx* in northern India use habitats dominated by intensive agriculture within open urban areas (Majumdar et al. 2016; Roberts et al. 2016). This also seems to be the case for *P. s. comorensis*. Indeed, our SDM analysis at a broad scale suggested a distribution strongly correlated to degraded forests, low elevations, and proximity to villages and roads. In addition, according to our ENFA at a fine scale, this species is relatively generalist in terms of use of vegetation cover. This may be explained by the fact that it feeds on a large diversity of plants (38 plant species) distributed over different types of habitats, including degraded forests, areas near villages and—principally—grasslands and

plantations (Trewhella et al. 2001). Our results confirm that this species uses a wide range of roosting plants (22 plant species), and that these plants are located in different types of habitats, including farmland. We found that *Ceiba pentandra*, *Pterocarpus indicus* and *Albizia* sp. were the plants most used by *P. s. comorensis* colonies for roosting (Table S1). These species are commonly found on agricultural land and in open areas.

We counted 11,898 *P. s. comorensis* in the three studied islands of Comoros. These results represent the first individual counting of the *P. s. comorensis* in Comoros to date. However, as the goal of our study was not to collect data regarding population size, but rather to collect presence–absence data for SDM modeling, we used a spatial sampling strategy that cannot be considered robust in terms of obtaining an unbiased estimation of population size. First, we did not systematically sample the islands. As this species has a relatively large distribution on the three islands, some colonies could have been missed. The method we adopted (consisting of visiting villages and interviewing the inhabitants) should allow a fairly accurate picture of major roosts, but we cannot exclude that some relatively small roosts might have been missed. Second, due to logistical constraints, it was not possible to conduct simultaneous counts at the island scale. Since bats can move between colonies, this could have led to double counts or to the underestimation of some roosts. Third, given that *P. s. comorensis* live in large colonies (of up to 700 individuals in our counts) and in some case in dense vegetation (for instance when the species live in sympatry with *P. livingstonii*), some individuals hidden by foliage might have been missed during the roosting counts. This lead to an underestimation of the population sizes. Our counts are not the true abundance of the species, but rather the minimum population size. It could, however, provide the basis for future monitoring of this species. Specific surveys such as a bat census on 1 km × 1 km randomly selected grids would be necessary to obtain reliable population data for the species.

The colonies of *P. s. comorensis* roosted in tall, old trees, probably because these can hold a large number of individuals and also because they better allow the bats to avoid human hunters. Yet a roosting preference for large, tall trees makes the species highly vulnerable as such plants are regularly cut down both in forests and near villages. For example, on Anjouan Island, the kapok trees (*Ceiba pentandra*) that hosted large numbers of *P. s. comorensis* in our counts experienced extensive felling between 1990 and 2000 for economic and political reasons, leading to a sharp decrease in abundance of *P. s. comorensis*. Traditionally, fruit bat species were protected by cultural taboos and were therefore not hunted by the local population. Yet according to our interviews with inhabitants (unpublished results), *P. s. comorensis* is currently hunted and eaten by villagers.

According to our results, although the roosting sites for *P. s. comorensis* are located in villages, near roads and in plantation areas, the foraging sites for this can also be located in natural forest at high elevation reaching 1200 m in the Anjouan Island. In the islands of Anjouan and Mohéli, although the suitable area for roosting site is estimated to 233 km^2, the suitable habitat for foraging sites is estimated to 506 km^2 (Fig. 7). This difference is explained by (1) the plasticity of the species in terms of resource use, especially due to the high diversity of plants used for food (Trewhella et al. 2001) but also probably (2) to its large population size that might lead individuals to spread over large area to avoid competition for food. The small suitable area for roosting sites (233 km^2 in Anjouan and Mohéli) is worrying because of the high rate of habitat disturbance in these islands.

These findings highlight that despite its relatively high abundance and large potential distribution range at global scale (600 km^2 according to our results using all the dataset), the viability of this species strongly depends on human practices that can rapidly evolve, and thus its viability is not guaranteed. The fact that this species occupies habitats close to

humans and largely depends on degraded habitats makes it particularly vulnerable to the risk of extinction due to regular hunting and roost disturbance through tree cutting. Currently, it is classified as a species of Least Concern (LC) in the IUCN Red List; however, we feel that a conservation campaign is urgently needed to secure its population viability. The two key conservation measures would be for the government to prohibit or regulate tree cutting, especially of trees such as *C. pentandra, Ficus* sp., etc. most used as flying fox roosts as this was suggested by Sewall et al. (2007), as well as to regulate hunting of bats.

Pteropus livingstonii

Pteropus livingstonii is a forest-dependent species restricted to the steep slopes of the remaining high-altitude forests on Anjouan and Mohéli Islands (Sewall et al. 2011a, b). Currently, colonies of this species are also found in some degraded habitats and agricultural lands located near these forests (Daniel et al. 2016). Our results based on ESMs and ENFA confirm the strong relationship between this species and the steep slopes of high-elevation forests. Three main hypotheses could explain this restriction to the slopes of these forests: competition with *P. s. comorensis*, the species' flight morphology traits, and lastly, 'real' selection of these habitats.

According to some previous studies, the restriction of *P. livingstonii* to high-altitude forests might be the result of competition behavior with the *P. s. comorensis* (Carroll and Thorpe 1991; Trewhella et al. 2001), which is far more abundant. In accordance with this explanation, our results show that the suitable habitat for the two species overlaps by only 7.4 km^2. Yet, our findings show that although both species share certain plant species for roosting, the majority of roosting plants are specific to each species, limiting competition. According to Trewhella et al. (2001) and our interviews with local people (unpublished results), although the two species show some overlap in food resource used, they largely feed on different plant species. So even if there is potential competition between the two species, it may not be strong enough to lead to the exclusion of *P. livingstonii* from low-elevation habitats.

Norberg et al. (Norberg et al. 2000) have mentioned that morphological traits of this species and its use of soaring flight might cause it to select steep slopes. Yet according to our interviews with the local population (unpublished results), this species was historically found near villages at low elevations when natural forests were still present. Moreover, no roosting sites for this species were found to be located on unforested slopes (Granek 2002). So this species' preference for slopes might be better explained by its selection of forest than by a selection for flight facility in relation to its flight morphology traits. Our SDM (at a broad spatial scale) suggests a strong relationship between the distribution of this species and natural forests. Additionally, according to our ENFA model (at plot scale), this species strongly selects habitats with a high plant density, while canopy openness is avoided. Together, these results suggest that *P. livingstonii* is highly specialized to a habitat with dense forest vegetation and avoids open areas. Moreover, according to Trewhella et al. (2001) and confirmed by our study, *P. livingstonii* uses a limited number of plant species for food and roosting (Table S2), and these are mostly restricted to the dense mid- and high-altitude evergreen rainforests of Comoros (Trewhella et al. 2001). This strong selection for natural forests could then indirectly explain the selection of slopes at altitude, since undisturbed natural forests in Comoros are largely restricted to relatively high elevations and steep slopes as these areas are inaccessible for wood harvesting or agriculture.

Our roosting counts recorded a total of 1243 individuals for this species in 19 visited roosts on two islands. In a recent paper, Daniel et al. (2016) suggested a total of 1260 individuals at 21 sites on the two islands for this species. Other previous roosting counts conducted in 1998 at 11 sites (Trewhella et al. 1998), in 2002 at 15 sites (Granek 2002), in 2007 at also 21 sites (Sewall et al. 2007) for this species suggested a total number of individuals of 400 and 1200-1500 and 1200 individuals respectively. Thus, all four studies provide a congruent total number of individuals except the study of Trewhella et al. (1998). The Trewhella et al. (1998) study detected a low number of individuals probably because some roosts were unknown since it represents the first study investigating the *P. livingstonii roosts*. In the other hand, some previous roosts might have splitted into several roosts. However, our population count resulted in some differences with the other two studies in terms of the number of individuals recorded at site scale. For instance, we estimated 349 and 104 individuals in the sites of Hassera-Ndregé and Hakidogo respectively (wet season 2015) against 45 and 3 individuals in the study by Daniel et al. (dry season 2012), and 80 and 15 individuals in the study by Granek (wet season 1998), 94 and 41 by Sewall et al. (2007) at the same sites respectively. Trewhella et al. (1998) estimated 60 individuals in the site of Hakidogo (Ouallah-Mirereni). Due to field difficulties, we cannot rule out the possibility of errors in our counts as they were carried out mostly in the rain during the wet season. Secondly, seasonal fluctuation of individual attendance at sites, as shown by Granek (2002) and Daniel et al. (2016) can also generate count differences. Lastly, as our survey was carried out 4 years after that of Daniel et al. and 20 years after the study of Granek, individuals might have moved to different sites: for instance, because of food availability (Nelson et al. 2000) or disturbances to roosting sites (Aziz et al. 2016). These latter two hypotheses are the most plausible explanation as the counts at island scale are congruent between the three studies. However, this congruence does not imply that the population size is stable as the number of known roosts increased over this time period from 15 (Granek 2002) to 21 (Sewall et al. 2007) without any increase in the overall population size.

As *P. livingstonii* is located in dense vegetation of natural forests, some individuals can simply be missed during the counting. Our numbers thus represents the minimum population size. The abundance of Livingstone's fruit bats was correlated with tall trees. Populations of this species occupied trees with a mean height of 23.60 ± 5.7 m and a mean dbh of 70 ± 20.1 cm. As for *P. s. comorensis*, individuals of this species roosted preferentially on large trees, limiting potential disturbance by humans (Luszcz and Barclay 2015). Other advantages of large trees are that they are able to host a large number of bats and have the potential to exist for a long time (Aziz et al. 2016). The disadvantage is that large, tall trees are those most sought after for harvesting, construction and other uses.

The range of the Livingstone's fruit bat (with the entire data set) was estimated to be 160 km^2 over the two islands of Anjouan and Mohéli (22% of the total surface area). This range consists largely of the remaining forests—natural or degraded. Our results represent the first evaluation of habitat suitability for *P. livingstonii* and *P. s. comorensis* using robust statistical methods. Sewall et al. (2016) estimated for *P. livingstonii* a range varying from 99.1 to 462.5 km^2 using minimum convex polygons method. Daniel et al. (2016) by using also the same method found a mean value of 113 km^2 for the same species. These slight differences observed between our results and those obtained by these different authors is explained by the difference in the methods used.

Unfortunately, with the exception of some sites on Mohéli Island that are currently managed by the Mohéli National Park, the remaining forests where *P. livingstonii* is found are highly disturbed by the local population, especially on Anjouan Island. The forests that remain on Anjouan still persist due to the fact that they are difficult for humans to access.

Yet given that the rate of habitat loss on these islands (8–9% per year) is estimated to be the highest in the world, that the human population is increasing on Anjouan (6.5% per year), and that the human population density was estimated to reach 517 hab/km^2 by 2016, it can be assumed that the range of *P. livingstonii* will significantly decrease in the near future due to the high demand for land use and intensive tree exploitation if conservation measures are not set up urgently. According to our results, the habitat requirement in the roosting and foraging sites is the same for *P. livingstonii*, both highly restricted in natural forest and high elevation. The long-term conservation strategy of these habitats is critically needed to ensure the viability of this species.

Both species of *Pteropus* are listed under the CITES. *Pteropus livingstonii* has recently been reclassified with a status of 'critically endangered' and *P. seychellensis* 'Least Concern' as on the IUCN Red List (Sewall et al. 2016). *Pteropus livingstonii* is nationally considered a high priority for conservation (Daniel et al. 2016). Extensive conservation actions were undertaken in the past by scientists and researchers (Sewall et al. 2007, 2016; Daniel et al. 2016). Yet the species receive little attention nowadays and there is little conservation work ongoing (Ibouroi, pers. obs.)

Implications for conservation management

The two flying fox species in the Comoros archipelago use different types of habitat and thus ensure different ecosystem services. The two species are not interchangeable—each plays a specific role in ecosystem functioning that is critical in maintaining the overall ecosystem dynamics. *P. livingstonii* appears highly threatened in the relative short term due to its low population abundance, its small spatial range, and the high rate of habitat loss in the Comoros. On the other hand, the population of this species is located on the steep slopes of high-altitude forests where access by humans is difficult. In addition, according to our interviews with the local population, this species is not hunted by Comorian people. In contrast, *P. s. comorensis* seems to be less threatened due to a high population abundance and large spatial distribution. Yet its dependence on degraded habitats and the high rate of hunting pressure and roost disturbance by local people could rapidly change its situation depending on human demographics, agricultural practices, and the local economy.

Many researchers have proposed actions to conserve Comorian biodiversity, especially concerning *P. livingstonii* (Trewhella et al. 1998, 2001, 2005; Granek 2000; Sewall et al. 2007, 2011a, b, 2016; Daniel et al. 2016). Some of these measures have been developed in collaboration with local, national, and international organizations such as the national "Action Comores" and the "Action Comores International". In 1992, Mickleburgh et al. (1992) developed a conservation plan in which the prevention of the extinction of fruit bats, including *P. livingstonii*, was among the top priorities. This proposal recommended different conservation strategies, including the long-term monitoring of the *P. livingstonii* population and the protection of both roosting and foraging sites for the species (Mickleburgh et al. 1992). The same authors also recommended environmental education for the population, the establishment of protected areas within the forest of Anjouan and Mohéli, and the establishment of a captive-breeding program for the species.

Later, other conservation plans were outlined in collaboration with the Comoros Government and the United Nations Development Program (UNDP 1998). These proposed, among other strategies, (1) a collaborative management framework for biodiversity conservation, including the conservation of *P. livingstonii* and marine turtles as the highest

priority in this conservation strategy, (2) the creation of a protected area on Mohéli Island, and (3) a program to increase awareness about biodiversity conservation as well as the establishment of livelihood activities that could generate income for local people and limit unsustainable use of natural resources. Granek (2000) also recommended the protection of both roosting and foraging habitats for *P. livingstonii,* highlighting that it is crucial to study variation in seasonal niche partitioning for the conservation of these species' habitats. In a later study, the same author recommended the establishment of a protected area within the habitat of *P. livingstonii* with the participation of the local population and village communities (Granek 2002). Sewall et al. (2007) went on to update the previous conservation plans to link together activities undertaken by local, national, and international organizations in one conservation network. The key objective was to ensure the continuity of conservation strategies to protect both *P. livingstonii* and its natural habitat, building on the measures previously developed by different scientists and NGOs and including (1) the protection of critical roosting and foraging habitats, (2) forest management, (3) environmental education to make local populations aware of the ecological importance of *P. livingstonii* and the rainforest for rural livelihoods, and (4) the continuation of *P. livingstonii* captive-breeding programs. Later, Sewall et al. (2011b) suggested protecting the 7 main roost sites of *P. livingstonii* through the development of a network of small community-managed forest reserves.

Of these different conservation proposals, some have been successfully developed, such as the creation of the Mohéli Marine Park in 2001, ongoing environmental education aimed at the Comorian local population, the establishment of a *P.livingstonii* captive-breeding program, the long-term monitoring of the *P. livingstonii* population, and the limitation of tree-felling in *P. livingstonii* roosting sites (Granek and Brown 2005; Sewall et al. 2007, 2011a, b).

Yet most of these implemented conservation strategies based on previous studies have focused on the protection of specific roost sites that host large numbers of *P.livingstonii*. Conservation actions have generally been implemented at a very local scale despite the recommendations provided by many researchers (Granek 2002; Sewall et al. 2007, 2011b). The problem is that very local actions are insufficient to ensure the broader conservation of these highly threatened species—local actions must be accompanied by national willingness and policies on a larger scale. And although some conservation measures have been taken, other proposals have not been achieved. For example, until 2016, no terrestrial protected areas had been established in the Comoros including the Anjouan Island where most *P. livingstonii* roosts occur and where the rate of habitat loss is the highest of the four islands (Boussougou et al. 2015). Despite the crucial efforts carried out by researchers and NGOs to educate local people about the environment and to raise their awareness about the importance of biodiversity conservation, the unsustainable use of natural resources continues.

Yet there is evidence that suggests that environmental education efforts carried out in the Comoros have been at least partially successful (Trewhella et al. 2005; Sewall et al. 2007, 2011a, b). For example, based on interviews we carried out with local people, although one of the two studied species (*P. s. comorensis*) is hunted by rural people for meat, the two species are generally seen as important pollinators and seed dispersers necessary for forest regeneration (unpublished results). Our findings indicate that Comorians have a generally positive perception of fruit bats, whereas in many countries these species are often viewed as pests of agriculture and fruit crops (Wordley et al. 2014; Aziz et al. 2016) and are often killed due to this negative perception (Korine et al. 1999; Aziz et al. 2016).

However, a wider problem is that Comorians seem constrained by poverty to heavily exploit forests. Thus reducing poverty and improving the subsistence conditions of the rural population are of prime importance in order to successfully implement long-term conservation strategies for biodiversity and habitats (Sewall et al. 2007). In the Comoros, the most effective conservation management plan would be to adopt programs that tackle poverty in communities near forests. This strategy could begin by addressing the needs of local people, allowing them to be less dependent on forest resources.

A project is currently being undertaken by the Comoros Government to create a national system of protected areas in the three Comoros Islands (SPANB/PA-COMORES 2016). If this were to include all the potential habitats of *P. livingstonii* and some roosting and foraging sites for *P. s. comorensis* located, for instance, in degraded or preserved forests on the islands of Anjouan and Mohéli, this would help to ensure the protection of both species. More specifically, we recommend making the forest of Hassera-Ndregé plus a 2-km zone around it a priority area inside the Mohéli Protected Area to ensure habitat and biodiversity viability on this island. On the island of Anjouan, we recommend making priority zones of the forest fragment located north of the villages of Nindri, Kowe and Moya; of the forest of Lingoni; and of the forest located northeast of the village of Bazimini and southeast of the village of Mpage and including these in the system of protected areas as this was suggested by Sewall et al. (2011b). These areas host almost the entire population of *P. livingstonii*, the majority of the population of *P. s. comorensis* and the endemic fauna and flora they depend on.

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